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Shrub encroachment of coastal ecosystems depends on dune elevation

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Abstract

Woody plant encroachment is influenced by interactions between the physical environment and vegetation, which create heterogenous microenvironments some of which favor shrub recruitment through mitigation of the abiotic environment. Encroachment of native shrub, *Morella cerifera* into grasslands on Hog Island, Virginia has been attributed to warmer winter temperature; however, recruitment of seedlings in grasslands may be impacted by multiple factors at the level of the microhabitat. Our study focuses on a critical gap in understanding factors specifically influencing *M. cerifera* seedling recruitment and survival. By experimentally planting *M. cerifera* seedlings at varying dune elevations and grass densities, we tested hypotheses that dune elevation influences the microclimate, soil characteristics and vegetation cover and that grass cover/density is related to shrub establishment. We tested these hypotheses through gathering data from temperature data loggers, conducting soil water content and chloride analyses, and determining percent cover of grasses relative to dune elevation. Results indicate that dune elevation was positively related to moderated temperatures with reduced temperature extremes and vegetation cover/composition that led to favorable locations for *M. cerifera* establishment and growth. Where dune elevation is >2 m, we document an upper limit of grass cover on natural seedling establishment, suggesting a switch from facilitative to competitive effects with grass density. Overall, our work demonstrates interactions between dune elevation and medium grass density has a facilitative influence on *M. cerifera* establishment and can be used for future predictions of shrub growth with rising sea-levels.

Keywords Shrub encroachment · Dune elevation · Grass density · Morella cerifera

Introduction

Woody encroachment into previously grass-dominated landscapes represents a regime shift observed worldwide, driven broadly by climate and land-use change (Ratajczak et al. 2017; Scharnagl et al. 2019). Transition from grassland to shrubland in ecosystems is in response to changes in multiple factors including high grazing pressure, suppression of wildfires, competition between grasses and shrubs and predator suppression (Li et al. 2022). These factors differ based on the ecosystem in which encroachment takes place. Regardless of ecosystem, shrubs are relieved of environmental constraints that once limited growth. For example, warmer winter temperatures have enabled the persistence of shrubs that were previously limited by freezing temperatures, facilitating encroachment into grasslands (D'Odorico et al. 2013; Archer et al. 2017). Coastal systems are particularly susceptible to the pressures of climate change as plant communities and ecological interactions are affected by both atmospheric (i.e., temperature and precipitation) and oceanic (i.e., sea-level rise and storm damage) drivers (Arkema et al. 2013; Zinnert et al. 2017). Warming temperatures (particularly in winter) have resulted in woody encroachment into coastal grassland and marsh (Battaglia et al. 2007; Lucas and Carter 2010; Saintilan et al. 2014; Osland et al. 2016; Zinnert et al. 2016; Huang et al. 2018).

Coastal ecosystems are naturally dynamic and constantly changing due to sediment movement, tides, and sea-level,

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all of which may affect woody encroachment. Feedbacks between vegetation and sediment deposition are critical for determining where shrub encroachment may occur (Zinnert et al. 2017; Franklin et al. 2024). Dune vegetation captures sediment, stimulating plant growth and resulting in dune formation on previously flat terrain. As dunes form and grow, they coalesce over time (Goldstein et al. 2017), preventing sediment and salt spray from reaching interior swales (Sabo et al. 2024). These processes result in a heterogeneous landscape, with woody species often establishing behind developed dunes (Woods et al. 2019; Bakker et al. 2023). In coastal systems, distinct vegetation zonation patterns are observed along a continuum from the shoreline landward, often determined by salinity and with a gradient of varying dune elevations. Thus, dune elevation appears to provide an important environmental filter on sediment and seawater movement, influencing vegetation dynamics beyond the dune (Zinnert et al. 2017; Schwarz et al. 2018; Woods et al. 2019). Dune topography affects disturbance frequency and severity that interior communities experience (Stallins 2005; Brown and Zinnert 2021; Sabo et al. 2024) and a minimum dune elevation of 1.75–2 m has been associated with shrub presence (Miller et al. 2008; Woods et al. 2019), but the role of dune elevation is unknown for preparing the microenvironment for successful shrub establishment and growth.

Along the mid-Atlantic and Gulf coasts, warming winter temperatures enhanced by microclimatic moderation have resulted in encroachment of *Morella cerifera* (wax myrtle), into previously grassland dominated communities (Battaglia et al. 2007; Lucas and Carter 2010; Charles et al. 2020; Wood et al. 2020). *Morella cerifera*, a native, evergreen with an obligate N-fixing actinomycete, *Frankia,* association has increased cover in coastal areas, resulting in dense thickets and does not increase bare ground often observed in many xeric communities (Huang et al. 2020; Schreiner-McGraw et al. 2020). When sea level rises, barrier islands typically move landward (i.e., island migration) due to overwash processes which deposit sediment onto the backbarrier marsh to maintain elevation above sea level. Woody encroachment disrupts the migration process by slowing down or blocking sediment movement into the interior and backbarrier marsh, resulting in increased shoreface erosion, and altering island response to sea-level rise (Zinnert et al. 2019; Reeves et al. 2022).

Although warming temperatures have facilitated *M. cerifera* expansion, our understanding of encroachment is limited to adult stages of development (i.e. above the grass canopy). A knowledge gap remains about the biotic and abiotic factors that determine successful establishment at early developmental stages. Shrub presence is positively correlated with dune elevation, observed behind dunes > 2 m in height (from dune toe to crest, Woods et al. 2019), but the mechanisms determining successful establishment are unknown. Previous grass removal experiments document that grasses facilitate shrub growth via temperature moderation at the microhabitat scale (Sinclair et al. 2020), but little is known about the effect of temperature on shrub establishment and seedling growth. Grass cover and density may be related to dune elevation and play a role in successful establishment following dispersal (Woods et al. 2019) but this has not been quantified. *Morella cerifera* has not been observed in bare sand habitat, despite presence of *Frankia* in the soils (Wijnholds and Young 2000). Dune elevation reduces salinity in the interior environment which can otherwise limit the germination and early growth of *M. cerifera* (Sande and Young 1992; Woods et al. 2000). Determining conditions necessary for successful *M. cerifera* establishment and growth will enable modeling of important ecological processes for predicting barrier island response to future climate scenarios (i.e., Rastetter 1991; Charbonneau et al. 2022; Reeves et al. 2022).

Multiple abiotic drivers and biotic processes operating synergistically or in tandem make forecasting ecosystem transitions (i.e., grass to shrub) difficult (Ratajczak et al. 2018). Growth and survival of shrub seedlings in local environmental conditions sets the trajectory of whether an enclosed canopy thicket forms (Zinnert et al. 2011; Huang et al. 2020). Here we quantify abiotic and biotic factors that support early shrub establishment due to differences in dune elevation. We use observational and experimental plantings on a Virginia barrier island to test the following hypotheses: (1) As dune elevation increases, the microclimate is modified with fewer temperature extremes, more favorable soil characteristics, due to higher vegetation cover and distance to the shoreline; (2) higher grass cover/density is positively related to shrub establishment (e.g., Woods et al. 2019). We quantified microclimate, survival and growth of naturally and transplanted *M. cerifera* seedlings in areas differing in grass density and behind dunes differing in elevation, low, embryonic dunes (maximum height 0–1.0 m), medium dunes (1.0–2.0 m), and high dunes (> 2.0 m).

Methods

Study site

Research was conducted on Hog Island (37.4183° N, 75.6935° W) in Northampton County, VA, USA, part of the Virginia Coast Reserve, a National Science Foundation funded Long-Term Ecological Research site owned and run by The Nature Conservancy. Hog Island has been uninhabited and undeveloped since the early 1930s. Hog Island is ~ 8 km from the Eastern Shore peninsula of Virginia, ~ 12 km long, and shrub encroachment has been well documented since the 1970s, with encroachment of woody species into grassland habitat from north to south on the island (Young et al. 2007; Zinnert et al. 2011; Woods et al. 2019). Mean annual temperature is 14.2 °C, ranging from a low of 2 °C to a high of 30 °C, and mean annual precipitation is 1065 mm with the highest occurring during the primary growing season of May to August (Brantley and Young 2010; Aguilar et al. 2012).

On the south end of Hog Island, Virginia, new sediment accretion has resulted in dunes varying in elevation (e.g., 1 m embryonic dunes, 1.5 m, > 2 m, Fig. 1), providing an opportunity to examine how the abiotic and biotic environment changes as dunes build. Transects perpendicular to the ocean shoreline (~ 150 m, n = 5) were established ~ 30 m apart in spring 2021 spanning three dune elevations (1 m, 1.5 m, > 2 m, measured from dune toe to crest) and three interdunal swales (n = 5). Along each transect, 10 × 10 m main plots (n = 3 per transect behind each aforementioned dune elevation) with subsample plots (n = 4, detailed below) were established in each swale for monitoring the variables that may impact shrub establishment.

Effect of dune elevation on the abiotic environment

Temperature data-loggers (iButton, Thermochron, Baulkham Hills, New South Wales, Australia), were placed in each grassland swale plot 10 cm above the ground. Temperature was recorded every two hours from June 2021 to June 2023 to determine average annual temperature and identify extreme temperatures experienced by seedlings. Daily and monthly minimum and maximum temperatures and the 10% coldest and warmest temperatures of all records were calculated.

Soils were collected from the top 20 cm in each 10 × 10 m plot (n = 30) during the autumn, summer, and winter from 2021–2022 for soil chlorides to determine salinity content using an Orion Research digital ion analyzer (model: 501, Orion Corporation, Espoo, Finland) that measured ionic conductivity (mV) of each sample and compared to known salinity standards. In summer 2023, soils were collected and kept in plastic bags to quantify soil moisture content, which

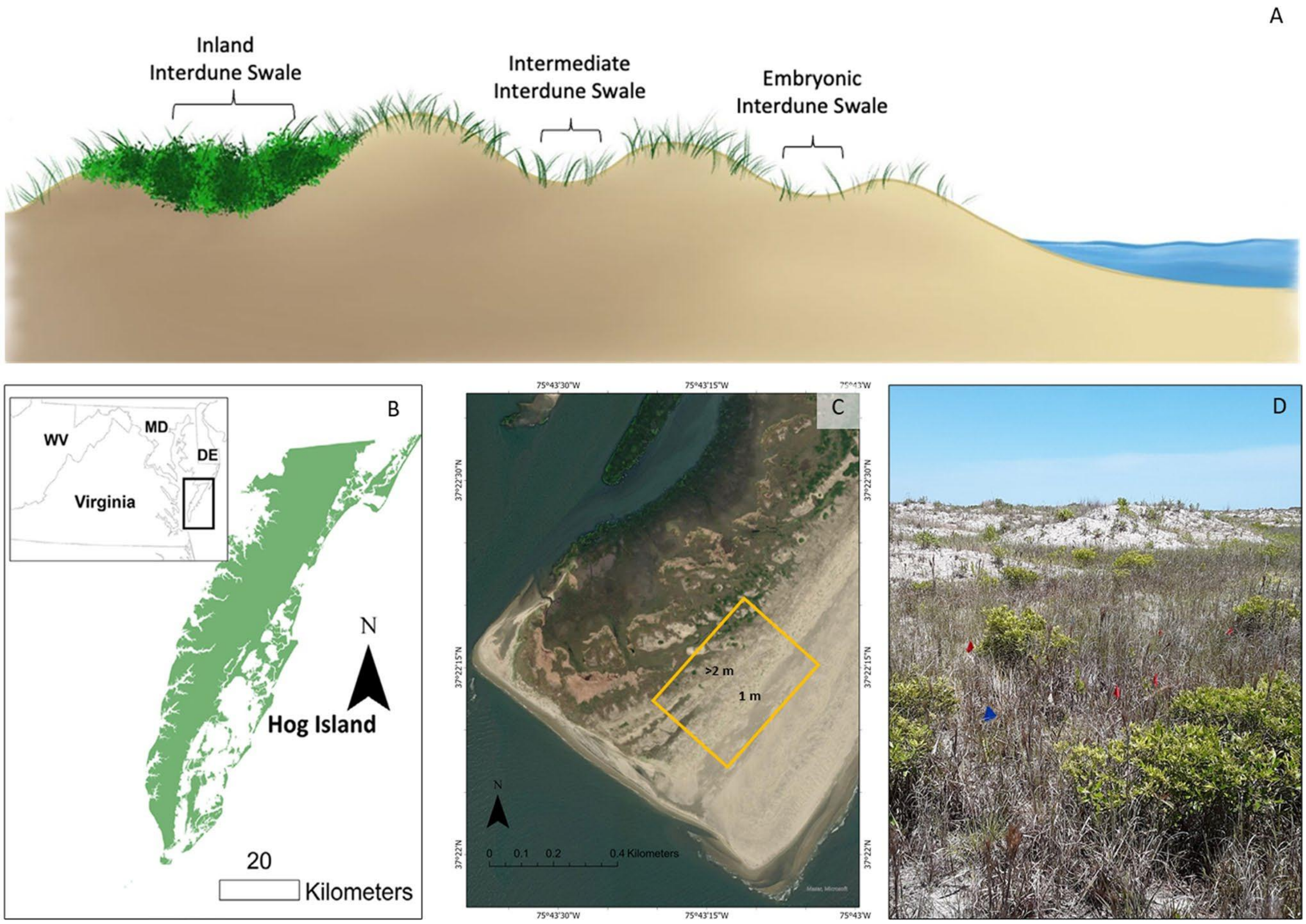

Fig. 1 **A** Schematic of swale locations behind dunes of different elevations. **B** Location of study site, Hog Island, Virginia. **C** Locations of study plots at the southern tip of Hog Island with 1 m and >2 m dunes noted in the image. **D** Inland interdune swale showing established Morella cerifera seedlings (>2 m dune visible in background of picture)

was determined by weighing cores to obtain water mass before and after drying at 105 °C for 72 h.

Effect of dune elevation on species composition and shrub growth

Vegetation composition, percent cover, and height of each species were randomly quantified in 1×1 m subplots ($n = 4$ per main 10×10 m plot). Species richness and Shannon Weiner diversity (H') were calculated from these data. Stem density was quantified for grasses and herbaceous species (no shrubs) in 10×10 cm quadrats within the 1×1 m subplots. Stem density was standardized to number of stems per m^2.

To determine the impact of dune elevation on *M. cerifera* establishment, seedlings from nearby swales were transplanted behind each dune elevation (1 m, 1.5 m, > 2 m) in June 2021 ($n = 30$ per dune elevation). Naturally occurring *M. cerifera* seedlings ($n = 47$ among all plots) found only behind the > 2 m dunes, were monitored with transplants. Height and maximum crown diameter along two perpendicular axes of all tagged *M. cerifera* seedlings (natural and transplanted) were measured during each of the following months: August 2021, January 2022, June 2022, and February 2023. Crown area was calculated using the equation for finding the area of an ellipse:

$$Canopy\,Area = \pi \times crown\,radius \times perpendicular\,radius$$

Growth rates of height and crown area were determined between summer and winter seasons (Jan 2022-Aug 2021, Jun 2022-Jan 2022, Feb 2023-Aug 2023) and standardized per number of days between sampling events.

$$height\,growth\,rate = (height\,2 - height\,1) / days$$

$$crown\,area\,growth\,rate = (area\,2 - area\,1) / days$$

Effect of grass density on shrub growth

To determine if grass density influenced seedling growth, additional plots (3×3 m) were established in swale plots behind > 2 m dunes in June 2022 that ranged from medium (36–70%) to high (95–99%) grass density ($n = 10$, 5 per density class). Measurements of light availability were made using a digital light meter (Zhu Hai Ouborui Electronic Co., Ltd, Zhuhai, China) in June 2022. Naturally occurring shrub seedlings ($n = 10$) were identified and tagged in plots where they occurred. Shrub seedlings ($n = 5$) found in nearby swales were transplanted adjacent to observational plots in medium (40–70%) and high (95–99%) grass density plots ($n = 10$). All seedlings were tagged and monitored for growth (plant height, maximum crown diameter) and survival from June 2022 to June 2023.

Statistics

Effect of dune elevation (natural and experimental)

Due to non-normality, soil chlorides were log-transformed for analysis and percent cover, stem number, and richness were log + 1 transformed to account for 0 s in the data. Repeated measures two-way mixed model analysis of variance (ANOVA) was used to determine effect of dune elevation and sampling month on minimum and maximum temperature. One-way ANOVA was used to evaluate differences in extreme temperatures and soil moisture by dune elevation. Two-way ANOVA was used to determine effect of dune elevation and season on soil chlorides. One-way ANOVA with subsampling was used to determine dune elevation effects percent cover, stem number, species richness, and Shannon–Weiner diversity. Herbaceous community composition based on species percent cover among the different dune elevations was visualized with nonmetric multidimensional scaling (NMS) using a Bray–Curtis dissimilarity matrix and three-dimensions. The program runs a sequence of eleven trials and automatically chooses the one with the smallest stress. The resulting plot was displayed on the first two axes. Species were included in the graph as weighted averages of the resulting row scores. Spearman's rank correlation was used to determine if *Morella cerifera* cover was correlated to resulting plot scores and grass species cover. PERMANOVA (9999 permutations) was used to determine if the herbaceous community differed among dune elevations. One-way ANOVA was used to evaluate differences in time on height and crown area growth rates for naturally occurring and transplanted seedlings. Pearson's correlations were used to evaluate the relationships among minimum and maximum temperatures, grass cover, average soil chlorides, and height/crown area growth rates of transplanted seedlings across the swales differing in dune elevation. JMP Version 16 software (SAS Institute Inc., Cary NC) was used for univariate statistical analyses and PAST4.16 (Hammer et al. 2001) was used for multivariate analyses.

Effect of grass density (natural and experimental)

The following variables were log-transformed due to nonnormality for analysis: growth rates of natural and experimental *M. cerifera* height and crown diameter. Linear regressions were used to determine effect of grass cover on shrub seedling number, species richness (excluding shrubs), and photosynthetically active radiation. Two-way ANOVA was performed to determine effect of grass density and time on plant height and crown diameter growth rates of natural and transplanted seedlings.

Results

Effect of dune elevation—natural community

Swales behind 1 m dunes experienced 8.9—10.6 ℃ warmer annual minimum (20.7 ℃ ± 0.1, mean ± standard error; 2-way ANOVA location: $F_{2,11297} = 19.5$, $p < 0.0001$) and 11.6–14.0 ℃ higher annual maximum (37.3℃ ± 0.3) temperatures (2-way ANOVA location: $F_{2,11297} = 50.5$, $p < 0.0001$, Table 1). There were no differences in minimum or maximum temperatures in swales behind 1.5 or > 2 m dunes. When examining the 10% coldest and warmest temperatures (i.e., extreme events), coldest temperatures were found in swales behind > 2 m dunes (− 3.2 ℃ ± 0.1, ANOVA: $F_{2,1021} = 93.6$, $p < 0.0001$) and warmest behind 1 m dunes (49.8 ± 0.1, ANOVA: $F_{2,1004} = 311.3$, $p < 0.0001$, Table 1). Swales behind 1 m dunes experienced a higher frequency of temperatures < − 6 ℃ and > 50 ℃ than swales behind taller dunes (Fig. 2). Behind 1 m dunes, temperatures up to 62 °C were recorded, whereas no temperatures > 54 °C were recorded in swales behind 1.5 and > 2 m dunes. Swale soils were generally dry (< 15% water content), but soils behind 1 m dunes were significantly lower in water content ($F_{2,15} = 11.9$, $p = 0.0008$, Table 1). Soil chlorides differed by season and site (2-way ANOVA: interaction: $F_{4,116} = 116.1$, $p < 0.0001$), with highest values observed in winter behind > 2 m dunes (1032 ± 223 μg g^{-1}, Table 1, Figure S1). During summer, soil chlorides were lowest.

Total vegetation cover increased with dune elevation (ANOVA: $F_{2,12} = 32.4$, $p < 0.0001$, Table 1) and was lowest behind 1 m dunes with < 10% cover compared to > 50% cover in swales behind dunes of higher elevations. Stem density (ANOVA: $F_{2,12} = 25.7$, $p < 0.0001$), species richness (ANOVA: $F_{2,12} = 37.2$, $p < 0.0001$), and H' diversity (ANOVA: $F_{2,12} = 18.9$, $p < 0.001$) significantly increased with dune elevation (Table 1). *Sporobolus pumilus* (Roth), previously named *Spartina patens,* was the only species found in all swales (Table S1). Community composition of herbaceous species cover was significantly different among all three swales (PERMANOVA: $\text{Pseudo-}F_{2,57} = 12.3$,

Table 1 Temperatures, soil moisture and vegetation measures of total percent cover, stem density, species richness and Shannon–Wiener diversity (H') across dune elevation gradients on Hog Island

Variable	1 m	1.5 m	> 2 m
Minimum temp (°C)	20.67 ± 0.11^b	10.01 ± 0.18^a	11.76 ± 0.20^a
Maximum temp (°C)	37.26 ± 0.27^b	23.26 ± 0.22^a	25.63 ± 0.24^a
Coldest 10% temps (°C)	-0.95 ± 0.13^a	-3.26 ± 0.11^c	-2.57 ± 0.11^b
Warmest 10% temps (°C)	49.84 ± 0.14^a	45.27 ± 0.11^b	45.27 ± 0.17^b
Soil moisture	2.3 ± 1.1^b	8.7 ± 1.8^a	11.8 ± 1.2^a
Soil chlorides (μg g^{-1})	67 ± 22^b	54 ± 18^b	251 ± 71^a
Total cover (°C)	9.8 ± 3.7^b	51.6 ± 5.5^a	84.3 ± 3.8^a
Stem density (°C)	40 ± 30^c	170 ± 30^b	240 ± 40^a
Species richness	0.6 ± 0.1^c	2.1 ± 0.3^b	3.9 ± 0.3^a
H' diversity	0 ± 0^b	0.4 ± 0.1^b	0.9 ± 0.1^a

VA Values represent mean ± SE

Letters represent statistical differences

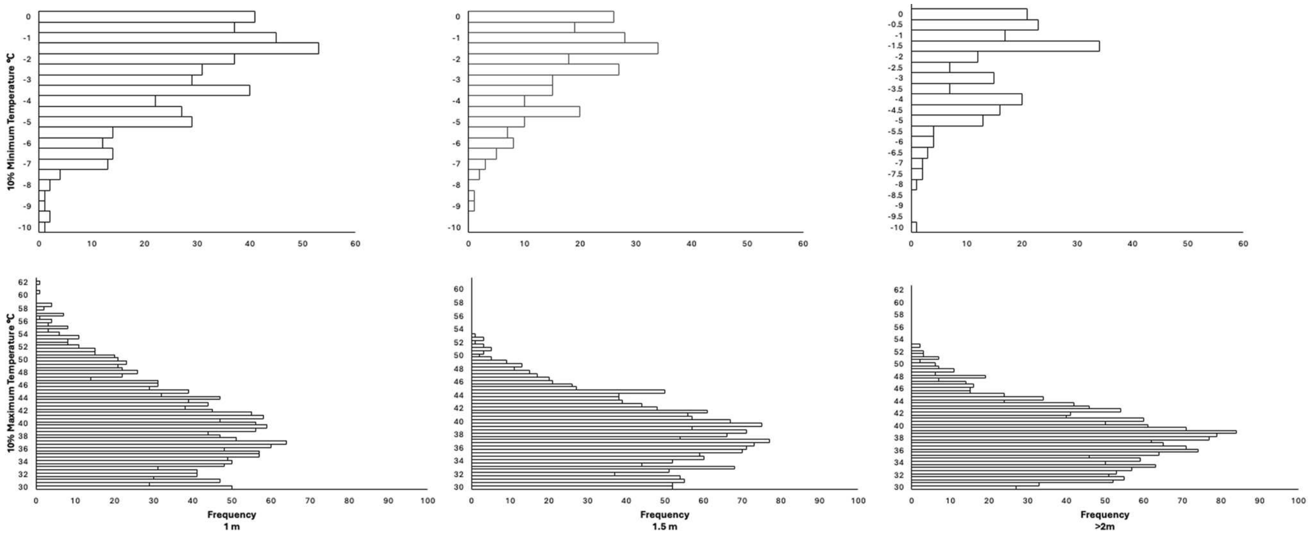

Fig. 2 Frequency of extreme minimum (top row) and maximum (bottom row) temperatures among the three interdune swales

$p < 0.0001$). When visualized with NMS (stress = 0.16), swales behind 1 m dunes were distinctly separated from the others, with a narrower range of community composition. Swales behind 1.5 m dunes exhibited a wide range of community composition, with overlap in swales behind > 2 m dunes (Figure S2). *Morella cerifera* cover was weakly associated with axis 1 ($r = 0.24$, $p = 0.01$). *Morella cerifera* cover was positively associated with *Panicum amarum* ($r = 0.38$, $p = 0.005$), *Solidago sempervirens* ($r = 0.57$, $p < 0.0001$), and *Borrichia frutescens* ($r = 0.48$, $p < 0.001$), and negatively with *Cakile edentula* ($r = -0.33$, $p = 0.02$).

Effect of dune elevation—experimental

No naturally occurring *M. cerifera* seedlings were documented in swales 1 m and 1.5 m dunes. Seedlings occurred only behind > 2 m dunes. Of seedlings that were transplanted in each dune swale, survival was > 60% during the first summer, but dropped to < 10% in 1.5 and < 1 m dunes by winter. After 2 years, transplant survival remained high behind > 2 m dunes (80%), whereas < 1% of transplants survived behind 1.5 and < 1 dunes (Table 2).

In naturally occurring and transplanted seedlings behind > 2 m dunes, greatest growth rates (height and crown area) occurred from winter to summer, a time when most plants are dormant (ANOVA: height, $F_{2,100} = 38.7$, $p < 0.0001$; crown area $F_{2,92} = 36.01$, $p < 0.0001$; Fig. 3). During this time, plants grew 0.08 ± 0.01 cm per day taller and crown area grew at a rate of 2.24 ± 0.34 cm^2 per day. In the summer to winter timeframe, the plant height growth rate was reduced by 37% (0.03 ± 0.01 cm per day) and the crown area growth rate was reduced by 66% (0.76 ± 0.19 cm^2 per day). The average growth rate of shrub height was negatively correlated with minimum ($r = -0.59$) and with maximum ($r = -0.41$) temperatures (Figure S3) but not grass density or soil chlorides.

Table 2 Survival of transplanted seedlings after three growing seasons in swales behind different dune elevations

Year	1 m (%)	1.5 m (%)	> 2 m (%)
Summer 2021	67	87	100
Winter 2022	3	7	83
Summer 2022	3	7	80
Winter 2023	3	7	80
Summer 2023	3	7	80

Effect of grass density—natural community

Shrub number was negatively correlated to grass cover with no seedlings observed when grass cover was > 95% (high grass density plots, $r^2 = 0.89$, $p < 0.001$, Fig. 4). *Sporobolus pumilus* was the only species found in high density grass plots (cover, 96.2 ± 1.8). As grass cover increased, light availability decreased with low light levels (< 400 μmol m^2 s^{-1}) observed in high density grass plots ($r^2 = 0.88$, $p < 0.0001$, Fig. 4). Lower levels of grass cover (medium density plots) had higher species richness ($r^2 = 0.77$, $p = 0.0009$) composed of grasses, one forb, and shrubs. Soil chlorides were low in all grass density plots, but a significant difference was found between high grass density (28.6 ± 2.4 μg g^{-1}) and medium density plots (37.9 ± 2.6 μg g^{-1}, $F = 6.6$, $p = 0.0166$).

Effect of grass density—experimental

During the first growing season following transplanting, survival of *M. cerifera* seedlings was > 80% in medium and high grass densities. After one year, *M. cerifera* seedlings survival rates were reduced in high grass density plots (24 ± 10%), while medium density plots maintained higher survival rates (68 ± 19%). There was no significant time x density interaction (2-way ANOVA interaction: $F_{2,54} = 0.89$, $p = 0.42$; crown area: $F_{2,49} = 0.41$, $p = 0.66$). Of plants that

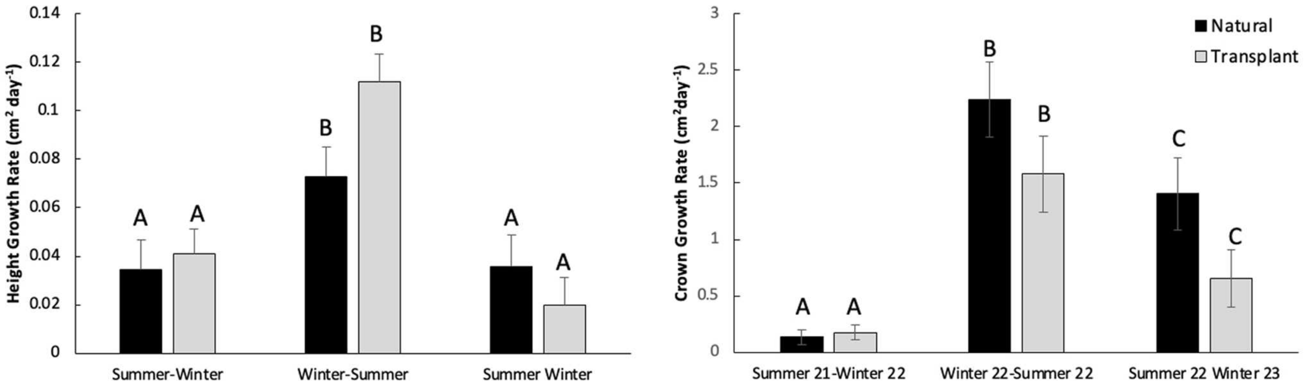

Fig. 3 Differences in height growth over different seasons for natural and transplanted seedlings in the interdune swale (>2 m) (left). Differences in crown growth over different seasons for natural and transplanted seedlings in the interdune swale (>2 m) (right)

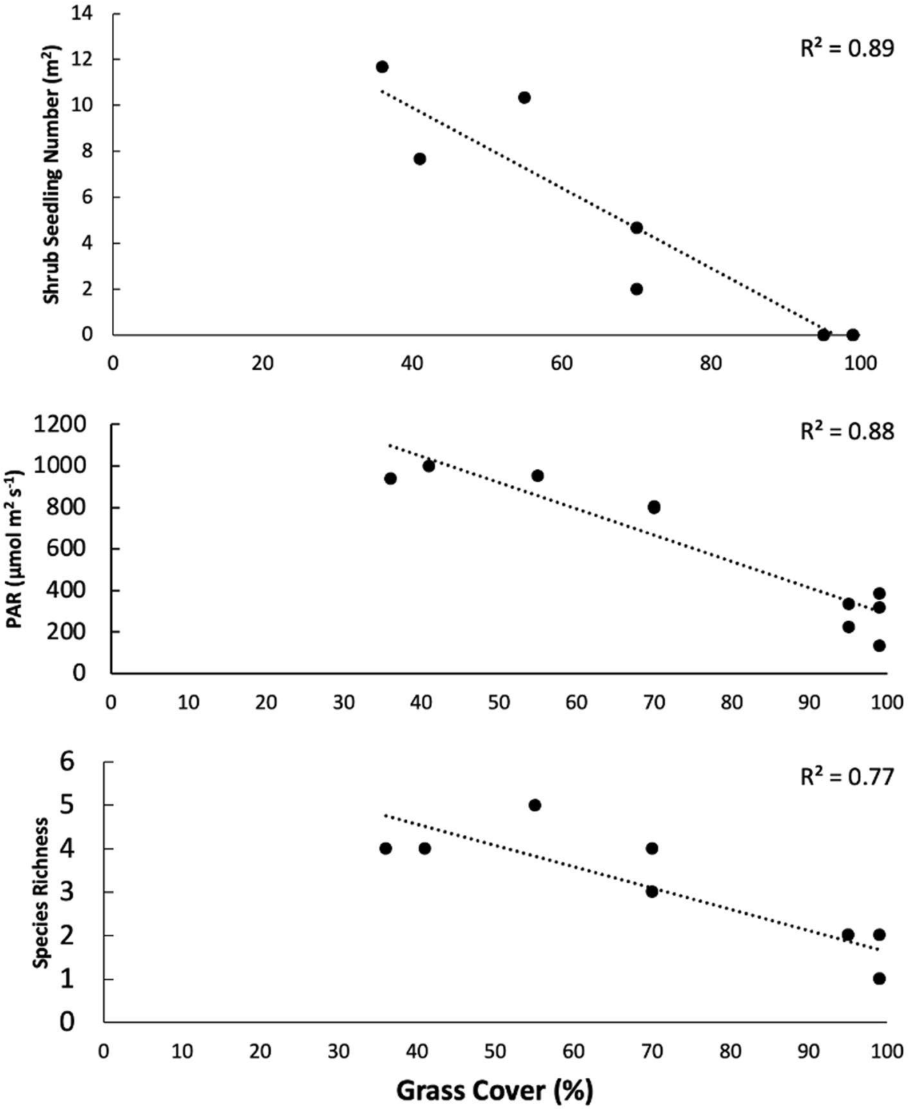

Fig. 4 Negative linear relationships were observed between grassland percent cover and shrub seedling number (top), PAR (middle), and species richness (bottom)

survived, there was no main effect of grass density on transplanted seedling height and crown area growth rates (height: $F_{1,54} = 2.61$, $p = 0.11$; crown area: $F_{1,49} = 0.13$, $p = 0.72$), but there was an effect of time on growth, which was highest during the winter to summer seasons (height: 0.12 ± 0.07 cm per day, $F_{2,54} = 21.01$, $p < 0.0001$; crown area: 1.58 ± 0.39 cm^2 per day, $F_{2,49} = 17.11$, $p < 0.0001$) relative to the summer to winter season (height: 0.03 ± 0.01 cm per day; crown area: 0.42 ± 0.15 cm^2 per day).

Discussion

In this study we found that dune elevation is the primary factor influencing vegetation composition, cover, and microclimate; however, when dune elevation is sufficient for shrub establishment (> 2 m), grass cover further modifies the environment and can limit shrub establishment and growth. We documented an upper limit of grass cover on natural seedling shrub establishment in this coastal system, suggesting a switch from facilitative to competitive effects with grass density. Many shrubs encroaching into grasslands are cold intolerant (Pockman and Sperry 1997; Krauss et al. 2008); however, macroclimatic warming and positive feedbacks with local microclimate are resulting in increased minimum nocturnal temperatures surrounding shrubs, creating a favorable environment for shrub growth (D'Odorico et al. 2010; He 2015; Huang et al. 2020).

Grassland temperature, density, and dune elevation were important factors impacting successful establishment of *M. cerifera*. Grass density was positively related to dune elevation which influenced the moderated annual, minimum, and maximum temperatures in interdune swales behind 1.5 and > 2 m dunes relative to those behind 1 m dunes. Similar results were found for temperature extremes, which are projected to become more frequent (Meehl et al. 2007). Extreme temperatures can limit seedling survival. Sinclair et al. (2020) found a threshold between − 6 and − 11 ºC at which seedling death occurs and net photosynthesis is reduced to 0 at temperatures > 50 ºC (Young 1992). Temperatures in swales behind 1 m dunes experienced more events that can limit survival and growth in *M. cerifera* with a greater number of events < − 6ºC and > 50 ºC.

Soil temperature, along with vegetation cover, is an important determinant of available soil moisture in freshwater limited environments (Lozano-Parra et al. 2018). Grass density was significantly highest behind > 2 m dunes, lowest in swales behind 1 m dunes, with 1.5 m dunes at intermediary levels. In the barrier island system, sandy soils retain little water resulting in low soil moisture (Osman 2018) as observed in our study. Our sampling did not allow us to determine explicit relationships between water availability and vegetation cover, but soil moisture collected at one timepoint during the summer (when *M. cerifera* transpiration is highest, Wood et al. 2020) was significantly lower (~ 2.3%) behind 1 m dunes. In a system reliant on precipitation for groundwater recharge, precipitation inputs are critical for growth and productivity at this time of year (Aguilar et al. 2012). Soil chlorides, which can limit the growth of successful germination of this salt sensitive species (Sande and Young 1992; Woods et al. 2020) were variable among all interdune swales; however, during this study, soil chlorides remained within the range that *M. cerifera* can tolerate (Young et al 1994) and less likely a limiting factor for seedling establishment in these locations.

Transplanted seedling growth rates were negatively correlated with both minimum and maximum temperatures across the three dune elevations and survival declined between summer and winter, but no relationship was observed with grass cover. Natural and transplanted *M. cerifera* seedlings persisted behind > 2 m dunes and experienced the greatest growth during the late winter—early summertime interval when other species are dormant. We were not able to discern strong abiotic differences (i.e., minimum/maximum temperatures, soil moisture) between interdune swales behind 1.5 and > 2 m dunes, but the occurrence and survival of *M. cerifera* in these locations was quite distinct. *Morella cerifera* did not naturally establish behind 1.5 m dunes, and when transplanted, only 7% of seedlings survived by the first winter. Although grass cover across all plots sampled was similar behind 1.5 and > 2 m dunes, species composition and diversity differed. Vegetation composition was more variable behind 1.5 m dunes and distinctly different, representing an intermediary between interdune swales behind 1 and > 2 m dunes. This suggests there is an interaction between dune elevation and grassland composition that leads to *M. cerifera* establishment that we were unable to quantify in this study.

Despite, this our results support studies demonstrating a minimum dune elevation threshold for successful *M. cerifera* recruitment (Miller et al. 2008; Woods et al. 2019). This dune threshold may also be necessary for higher species diversity and grass density as well. The role of freshwater availability via the depth to groundwater and soil moisture over time may be critical for determining successful establishment for *M. cerifera*. Dune elevation also influences the ease with which seawater can move into the island interior, with lower dunes (1.75 m) more susceptible to overtopping during high storm surge events compared to > 2 m dunes (Sabo et al. 2024). The frequency with which we were able to monitor soil chlorides may have missed events that resulted in seawater inundation and could limit shrub establishment. Higher temporal resolution sampling of soil moisture and soil chlorides may help identify limits on shrub establishment behind 1.5 m dunes.

In areas where dune elevation is sufficient to reduce inundation events (> 2 m), species can establish and further modify the environment, resulting in microhabitat heterogeneity where facilitative and/or competitive interactions occur (Callaway et al. 2002; Brown and Zinnert 2021; Sabo et al. 2024). In our study moderate grass cover (40–70%) was positively related to the number of naturally established *M. cerifera* seedlings found only behind > 2 m dunes. High grass cover (> 95%) limited the establishment of natural *M. cerifera* seedlings and survival was low (24%) for transplanted seedlings. For transplanted seedlings that did survive in high density plots, seedlings showed similar growth rates to those transplanted in lower grass density. Although seedlings are likely facilitated at moderate grass density (Sinclair et al. 2020) found behind > 2 m dunes, there is an upper limit at which grass density has a competitive effect and excludes *M. cerifera* seedling establishment and herbaceous plant species richness through light limitation and/or competition for water or other critical resources (Archer et al. 2017). Thus, even behind > 2 m dunes, grass density provides an important constraint on the environment that determines *M. cerifera* survival and growth.

Conclusions

Interactions between dune elevation and grass density have a pronounced influence on *M. cerifera* establishment. Dune elevation appears to be the primary modifier on both the abiotic and biotic environment. Dune elevation > 2 m results in a modified abiotic environment, allowing for higher grass density, moderated temperatures, and successful shrub seedling establishment. We found an upper limit of grass cover (95%) which competitively excludes *M. cerifera* establishment, possibly due to light limitations for seedlings, although further study is needed to determine this. In a system where shrubs have a significant impact on ecosystem function (i.e., island response to sea-level rise, carbon storage, Zinnert et al. 2019; Reeves et al. 2022; Wood et al. 2024), understanding the limitations to shrub growth can inform future predictions of shrub growth as sediment is constantly redistributed. This work has important implications for dune restoration where woody species would naturally occur.

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Data availability Data availability statement: Data available through the VCR-LTER Data Catalog http://www.vcrlter.virginia.edu/cgi-bin/showDataset.cgi?docid=knb-lter-vcr.392 or upon request.

Declarations

Competing interests The authors declare no competing interests.

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